

Movement patterns of a specialist predator, the weasel *Mustela nivalis* exploiting asynchronous cyclic field vole *Microtus agrestis* populations

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Brandt M. J. and Lambin X. 2007. Movement patterns of a specialist predator, the weasel *Mustela nivalis* exploiting asynchronous cyclic field vole *Microtus agrestis* populations. Acta Theriologica 52: 13–25.

We investigated habitat selection and movement characteristics of male weasels *Mustela nivalis* Linnaeus, 1766 during the breeding season through radio-telemetry in Kielder Forest (KF) in order to assess how weasel movement is influenced by prey dynamics, mate searching and predation risk, and whether the scale of weasel movement corresponds to the spatial scale of the asynchronous, multi-annual vole population cycles observed in KF. Weasels used habitats with a high proportion of grass cover to a much larger extent than habitats with less grass cover and moved through the latter habitats faster and / or straighter. Habitats with high amounts of grass cover also had the highest field vole abundance, although total rodent abundance did not differ between habitats. The selection of this habitat by weasels might reflect weasels preferring field voles as prey or avoiding habitats with little grass cover and high intraguild predation risk. Five out of 8 male weasels radio-tracked had low day-to-day site fidelity and moved between different clear cuts. Three other males were resident in a single clear cut. This variation may reflect mate searching by male weasels. The observation that most weasels (5 out of 8) roamed over large areas and the scale of their dispersal potential suggests, that if they regulated vole populations, they should have a greater synchronising effect on the spatial scale of vole population dynamics than what is observed in vole populations in KF.

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Keywords: *Mustela nivalis*, population cycles, predation, home range, movement, weasel

Introduction

Specialist predators rely heavily on just one or very few prey species. The population dynam-

ics of a food-limited specialist predator ought to be closely linked to that of its prey. By definition and unlike generalist predators, they typically do not respond to decreases in prey numbers by switching to alternative prey. Specialists with

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low spatial mobility will show population dynamics similar to that of their prey. However, as the reproduction cycle of predators is usually longer than in their prey, their numerical response is expected to be time delayed. Cyclic dynamics of *Microtine* species have long been recognized, and predation by weasels *Mustela nivalis* Linnaeus, 1766 is regarded as a likely explanation, the so-called specialist predation hypothesis (SPH) (Andersson and Erlinge 1977, Hanski *et al.* 2001, Hanski and Henttonen 2002). Weasels are considered as a specialist predator due to the predominance of voles in their diet and their relative small spatial mobility (Andersson and Erlinge 1977). They are contrasted with nomadic avian predators, which also specialise on hunting small rodents but can travel long distances and should thus have a more synchronising effect on vole population dynamics. This is because by being more mobile, avian predators can respond to vole population declines by moving to areas of higher vole density rapidly hence tracking the abundance of their prey without any time delay (Andersson and Erlinge 1977, Ydenberg 1987, Ims and Andreassen 2000).

Field voles *Microtus agrestis* in Kielder Forest (KF) in northern England undergo multi-annual cycles that resemble those occurring in Fennoscandia with respect to the regularity of density changes over several years (Lambin *et al.* 2000). A removal experiment of weasels, however, did not support a key assumption of the SPH (Graham and Lambin 2002). Naturally-occurring and experimentally-induced variation in weasel abundance only explained a small fraction of variation in field vole survival. Weasel population dynamics in un-manipulated control sites, where weasels were not removed, also differed from what was expected under SPH. Weasel numbers showed seasonal dynamics with little year-to-year changes in abundance instead of a time-delayed numerical response (Graham 2001). This suggests that weasel density might not be solely limited by food supply in this area. Similar findings were reported by Jędrzejewski *et al.* (1995) for weasels in deciduous woodland in Białowieża, Poland.

Field vole population dynamics in KF differ from those observed in northern Fennoscandia in two key aspects. They show a smaller degree of spatial synchrony, and minimum density at the trough of cycles is much higher than in Fennoscandia (Lambin *et al.* 2000). In KF field vole populations in clear cuts separated by distances greater than 6 km tend to have asynchronous dynamics (Lambin *et al.* 1998), with asynchrony at even smaller scale in recent years (Bierman *et al.* 2006). If weasels were sufficiently mobile to reach those clear cuts where vole numbers are sufficiently high, they may not experience food shortage. As the extent of spatial synchrony in vole dynamics in KF is much smaller than in Fennoscandia, weasels in KF might act in the same way as nomadic avian predators do in Fennoscandia. They might not show a time-delayed numerical response because their number would not decline through starvation and subsequently rebuild, but individuals may instead simply avoid food limitation by moving between clear cuts of different vole densities. In effect, they could exploit asynchronous field voles populations as if they were alternative prey (Boutin 1995).

In this paper, we present information on weasel movement patterns in a heterogeneous environment, where grassy clear cuts are surrounded by mature forests or young clear cuts covered with brushwood left behind after felling and that completely lack any grass cover. We expected weasels (1) to have larger home ranges at clear cuts with lower field vole densities, (2) to select habitat with the highest field vole densities (3) to readily move between clear cuts in areas of low field vole density and (4) to show spatial movement that is greater than the spatial synchrony found in field vole population dynamics. We discuss our findings in relation to the potential impact of weasels on vole dynamics.

Material and method

Study area

The study was carried out in Kielder Forest (55°13'N, 2°33'W), Northumberland, UK, a large man-made conifer-

ous forest managed for commercial timber production. The dominating tree species are Sitka spruce *Picea sitchensis*, Norway spruce *Picea abies* and Larch *Larix* sp. The area is managed by rotational clear cutting. After clear cutting, brushwood is left behind such that it takes approximately three years for grass cover to develop. This leaves large clear cut patches of varying ages with many clear cuts dominated by grasses, mainly *Deschampsia caespitosa*, *Agrostis tenuis* and *Juncus effusus*, 3 years after felling. Clear cuts varied in size between 5–100 ha and mean distance between their outer edges was estimated as 177 m (Sherratt *et al.* 2000). Approximately 12 years after tree-planting forested areas no longer have dense grass cover due to light no longer penetrating to the ground through the closing canopy. The dominant rodent species is the field vole *Microtus agrestis*, but bank voles *Clethrionomys glareolus* and wood mice *Apodemus sylvaticus* also occur. The most abundant predators apart from weasels are red foxes *Vulpes vulpes*, common buzzards *Buteo buteo* and tawny owls *Strix aluco*. Field vole density varies widely (range 14–650 voles/ha) between clear cut patches (Lambin *et al.* 1998, Lambin *et al.* 2000).

Live trapping, handling and radio-tracking of weasels

We selected 6 clear cuts where tree-felling had taken place more than 5 years ago and which were dominated by *D. caespitosa* and *J. effusus*. Weasels were live-trapped using wooden flip-door boxes, built following King (1973) and baited with previously frozen fish, sawdust soiled with vole urine, straw and pieces of carrot for rodents caught incidentally. Twenty-five traps were spaced evenly throughout each of these clear cuts with a distance of about 50 m between them. Traps were preferentially placed in vole runs or close to linear features such as ditches, stonewalls or fences. Clear cuts, where weasel trapping was carried out, varied between 10–50 ha in size, although the trapped area never exceeded 15 ha within the larger clear cuts for logistical reasons. Clear cuts, where weasels were eventually radio-tracked, varied between 3–30 ha in size with an average

of 16 ha. Traps were checked daily and all non-target species were released, whilst weasels were returned to the laboratory for handling. Date, site and trap position were recorded for each weasel and all other vertebrates caught. Weasels were anaesthetized in the laboratory with 1–2 ml HalothaneTM. Under anaesthesia, body length and weight were measured and canine tooth wear recorded as a relative age indicator. Weasels were sexed from external appearance. Radio collars (BiotrackTM, Dorset, UK) weighting between 3.5 and 4.5 g (about 4% of a weasel's body weight) were fitted around the weasels' neck. Weasels were then kept in a holding tank, given a dead field vole and released 12–24 hours later at the site of capture, after they had eaten the vole. All procedures were carried out under a UK Home Office license and were also approved by Aberdeen University Animal Ethics Committee. Signal range of the radio transmitter was between 100 and 400 m depending on terrain and vegetation. Weasels were usually followed at a 10–30 m distance without any obvious impact on their behaviour. Weasels were followed continuously during the day as they were found to be largely inactive during the night (Brandt and Lambin 2005). Their location was determined at 15 minutes intervals by cross-triangulation and with the aid of a GPS GarminTM 12. Weasels were tracked until either the transmitter failed or contact was lost because the weasel had left the study area and could not be found. The location error, as indicated by the GPS was typically in the order of 10 m. Habitat type for each location was recorded by visually scoring grass cover (including sedges) in a 5 m radius around the point where the weasel had been located. Habitats were classified into 5 types depending on how much grass they provided. These types were as follows: type 1: 0–20%, type 2: 21–40%, type 3: 41–60%, type 4: 61–80%, type 5: 81–100% grass cover. For each fix we also recorded whether a weasel had been mobile or static during the previous 15 minutes.

In total, we radio-tracked 9 male common weasels, 1 of which was tracked in June 2001, and 8 of which were tracked between April and September 2002. We obtained a total of 2331 fixes over 69 days. Tracking was curtailed by premature radio failure for four of these weasels. Details on each weasel's capture dates, radio-tracking periods and

Table 1. Summary of biometrics, tracking period, vole density and fate of male weasels radio-tracked in this study. Weasel no 7a and 7b refer to the same individual tracked during two different time periods.

Weasel ID	Weight (g)	Body length (cm)	Period tracked	Days tracked	Vole density (voles/ha)	Fate
1	110	272	26 June–12 July 2002	17	151	disappeared
2	158	268	19–23 July 2002	5	193	radio failure
3	114	255	19–26 August 2002	7	123	probable radio failure
4	97	242	11–27 September 2002	11	161	radio failure
5	102	273	7–13 August 2002	7	66	radio failure
6	106	233	29 April–5 May 2002	4	81	disappeared
7a	135	238	25–26 July 2002	2	38	collar slipped off
7b	120	261	6–7 September 2002	2	94	died
8	58	200	18–24 September 2002	8	151	taken by raptor
9	116	280	20–27 June 2001	6	128	disappeared

biometrics are given in Table 1. Due to the very low capture rate of female weasels in this study we had to restrict this study to male weasels only.

Measuring field vole density

To gain an estimate of field vole density within a clear cut patch, we followed the grass-clipping-based method described by Lambin *et al.* (2000). We searched 25 randomly placed quadrates (25×25 cm) for the presence or absence of fresh grass clippings, which are the most reliable signs of current field vole presence. Vole signs were recorded within the optimal field vole habitat (corresponding to habitat types 4 and 5 above) of a clear cut. This vole sign index (VSI) was then converted into numbers of voles per ha using a calibration method based on live-trapping data and explaining 67–72% of the variance in vole densities (Lambin *et al.* 2000). Vole density estimates were obtained every month on each site except for the site where weasel no. 7 was tracked. In the analyses below, we used the field vole density estimate that was closest to the period at which weasels were tracked to a maximum interval of four weeks. These vole density estimates were used to test the influence of vole density on weasel home range, step length, distance between centres of activity and total distance travelled per day.

The VSI method is only calibrated for optimal habitat patches containing much grasses and sedges. We therefore used live-trapping to compare field vole density between different habitats and to estimate the density of other rodent species (bank voles and wood mice) within these habitats. Rodents were live-trapped using Ugglan Special mouse live traps baited with oats and carrots. Traps were distributed in a 15×15 m plot with 3 traps at each corner, using a widely used small quadrat technique (Myllymäki *et al.* 1971). Traps were placed in vole runs if possible and checked every morning. Caught animals were marked with ear-tags and with PIT-tags (as ear tags were sometimes lost), sexed, weighed and then released. Each trapping session lasted over 3 consecutive days. Habitat type was assessed by scoring the habitat within a 30 m quadrat centred on each trapping plot. The same visual habitat scores (habitat types 1–5) as during radio-tracking were used (see above). The number of field voles per trapping plot was calculated as a relative measurement of field vole density within different habitat types.

Habitat assessment

For analysis of habitat usage, the area over which a weasel ranged was mapped using a GPS. Habitat categories were assessed on a broader spatial scale than during telemetry. Due to forestry practices, patches of habitats were relatively homogeneous as they included clear cuts or replanted areas of given ages. We visually estimated the relative amount of grass cover for each separate clear cut or forested patch and categorized them as during radio-tracking (habitat types 1–5, see above), but applying the habitat categorisation to a broader spatial scale.

Home range and movement analyses

For home range and movement analyses we used the software Ranges 5. We calculated 100% minimum convex polygon home ranges (MCP) and core weighted Kernel home ranges. As weasel home ranges in the literature are mostly reported as MCP, we used this method to compare our results to other studies. Daily home ranges were calculated following the 100% minimum convex polygon method. Overlap between daily home ranges was calculated as the mean percentage of overlap between all possible pairs of daily home ranges per weasel. Other movement parameters (Table 3) were calculated as means for each weasel. The mean of all weasels tracked was calculated over the means of all individual weasels. Weasel step length was calculated as the straight line distance between two successive location fixes.

Statistical analyses

For analysis of daily movement patterns we excluded data from the day of release, when weasels might have shown biased movement patterns due to capture and handling procedures. For the calculation of total home range size, data of all 9 radio-tracked weasels were included. Weasel no. 8 was excluded from habitat analyses because habitat data were not available. For analyses of daily movement per weasel, weasel no. 7 was excluded as it was tracked at two different times and, after removing the two days of release, only 2 days remained which were spaced a month apart. For analyses of daily home range size and distance travelled per day, only days at which weasels were tracked for at least 4 h and were active for at least 1 h were included. For habitat analyses on the home range scale, habitats 4 and 5 were combined because only one weasel used habitat 5. Habitat analyses were conducted as described in Neu *et al.* (1974) and White and Garrott (1990). We compared available and utilised habitat using a Chi-square test to test whether individual weasels showed habitat selection and used Bonferroni confidence intervals to identify which habitats were avoided and selected by each individual. Habitat availability was calculated as the proportion of each habitat within weasel MCP home ranges while utilisation was calculated as the number of locations in each of these habitat types. Linear regression analysis was applied to test for influences of habitat scores on rodent densities and for the influence of total field vole density within a clear cut on weasel movement parameters. For statistical analyses we used the statistical software package SPSS 9. All tests were two-tailed.

Results

Prey availability in differing habitats

There was a statistically significant positive relationship between habitat score, and hence the amount of grass cover a habitat provided,

and the number of field voles trapped ($r_s = 0.59$, $n = 42$, $p < 0.01$) (Fig. 1a). No such effect was found with the number of bank voles ($r_s = -0.14$, $n = 42$, $p = 0.4$) and wood mice trapped ($r_s = -0.2$, $n = 42$, $p = 0.23$) (Fig. 1b–c). When all trapped rodents were pooled, there was also no evidence that the number of rodents significantly increased with habitat score ($r_s = 0.16$, $n = 42$, $p = 0.13$) (Fig. 1d).

Weasel habitat selection

All weasels showed significant habitat selection and did not use available habitats that had only a small proportion of grass cover (Table 2). All 7 weasels whose MCP home ranges encom-

passed habitat 1 (less than 20% grass cover) were never located in it. Four out of 5 weasels with habitat 2 in their MCP home range were not recorded using it while 1 weasel selected it. Habitat 3 was not used by 2 weasels, selected by 2 while 1 weasel showed no preference. For habitat 4 and 5 combined, 5 weasels used it more than expected while 2 used it according to its availability (Table 2).

Weasel trapping

Weasel trapping on these 6 clear cuts over at least 5 days each month between March and October 2002, yielded 23 individual weasels caught (18 males and 5 females), of which only 3 males

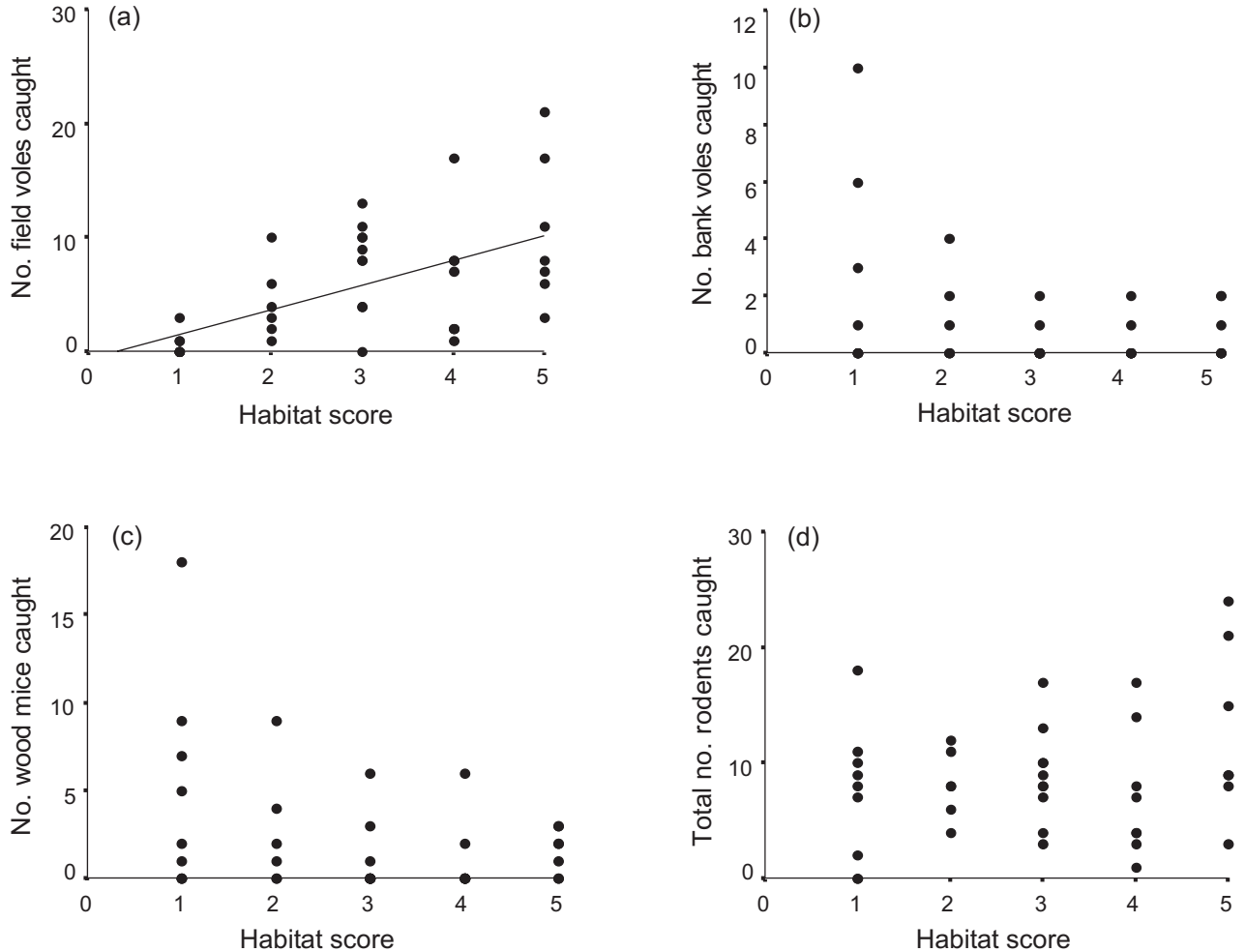


Fig. 1. Number of rodents (a – field voles, b – bank voles, c – wood mice, d – all species combined) caught per trapping grid plotted by habitat type (with habitat: 1 – 0–20%, habitat 2 – 21–40%, habitat 3 – 41–60, habitat 4 – 61–80% and, habitat 5 – 81–100% grass cover).

Table 2. Calculations of the χ^2 Statistics (Test for Preference) for weasel habitat selection (a – avoidance, p – preference). Expected no of locations are derived from the proportion this habitat contributed to 100% MCP home ranges of these individuals.

Weasel ID	Habitat	Observed no. of locations	Expected no. of locations	χ^2	p	Locations (%)	Confidence interval	Preference
1	1	14	163	136.674		0.0278	$0.00963 < p_1 < 0.04637$	a
1	2	179	124	24.680		0.3559	$0.30268 < p_2 < 0.40932$	p
1	3	230	182	12.608		0.4573	$0.40152 < p_3 < 0.51248$	p
1	4	80	34	63.606		0.1590	$0.11828 < p_4 < 0.19972$	p
Total		503		237.569	< 0.01			
3	2	15	42	17.148		0.0833	$0.03377 < p_2 < 0.13223$	a
3	3	1	10	8.536		0.0056	$-0.00780 < p_3 < 0.01980$	a
3	4	164	128	10.254		0.9111	$0.86019 < p_4 < 0.96181$	p
Total		180		35.938	< 0.01			
4	1	0	5	4.896		0.0000	$0.00000 < p_1 < 0.00000$	a
4	3	8	18	5.192		0.0392	$0.00655 < p_3 < 0.07145$	a
4	4	196	182	1.148		0.9608	$0.92855 < p_4 < 0.99345$	p
Total		204		11.236	< 0.01			
5	1	7	261	247.410		0.0158	$0.00171 < p_1 < 0.03029$	a
5	2	3	34	27.860		0.0068	$-0.00250 < p_2 < 0.01649$	a
5	4	432	147	551.133		0.9774	$0.95993 < p_4 < 0.99407$	p
Total		442		826.402	< 0.05			
6	1	0	152	152.256		0.0000	$0.00000 < p_1 < 0.00000$	a
6	4	312	160	145.119		1.0000	$1.00000 < p_4 < 1.00000$	p
Total		312		297.375	< 0.01			
7	1	1	11	9.230		0.0096	$-0.01437 < p_1 < 0.03437$	a
7	2	5	43	33.562		0.0481	$-0.00436 < p_2 < 0.10036$	a
7	3	93	46	49.176		0.8942	$0.81860 < p_3 < 0.96939$	p
7	4	5	4	0.132		0.0481	$-0.00436 < p_4 < 0.10036$	ns
Total		104		92.100	< 0.01			
8	1	1	19	16.630		0.0093	$-0.01276 < p_1 < 0.03076$	a
8	3	56	51	0.565		0.5185	$0.40390 < p_3 < 0.63409$	ns
8	4	51	39	3.856		0.4722	$0.35700 < p_4 < 0.58700$	ns
Total		108		21.051	< 0.01			
9	1	33	70	19.869		0.1875	$0.11750 < p_1 < 0.25851$	a
9	2	5	2	5.965		0.0284	$-0.00177 < p_2 < 0.05777$	a
9	4	138	99	15.116		0.7841	$0.70974 < p_4 < 0.85826$	p
Total		176		40.949	< 0.01			

were ever recaptured. Captures and recaptures were 8, 22 and 44 days apart and always occurred at the same clear cut where the animal was initially captured.

Weasel home ranges and movement patterns

Incremental analyses for Kernel home ranges yielded saturation for weasels no. 3, 4 and 5. Home range size for weasel no. 2 tended to level off at about 200 fixes, whereas for weasels no. 1,

6, 7, 8 and 9 saturation was not achieved. The results for the two different methods of calculating home range size are given in Table 3 together with information on the other movement parameters investigated. MCP home ranges varied from 6.5 to 67.8 ha (mean 26.3 ± 20.1 ha, $n = 9$) and Kernel home ranges varied from 4.1 to 45.4 ha (mean 22.9 ± 20.1 ha, $n = 9$). The area of habitat with more than 40% grass cover (habitat 3–5, which is the habitat weasels mainly used and might thus be termed “exploitable habitat”) in-

Table 3. Summary of movement parameters for weasels tracked in this study.

Weasel ID	MCP home range (ha)	Kernel home range (ha)	MCP without habitat 1 and 2 (ha)	Mean daily MCP (ha)	Mean % overlap between daily MCP's	Mean distance between centres of activity (m)	Mean total distance travelled/day (m)	Mean step length/15 min (m)
1	67.8	45.4	29	2.1	7.1	309	525	35
2	6.9	4.7	5.3	3	35.6	97	882	43
3	20.9	22.5	20.4	4.4	35.1	154	817	52
4	43.8	27.2	14.5	6.5	25.9	193	273	40
5	12.5	22.6	6.3	2.9	11.9	247	541	28
6	19.8	39.6	9.4	1.7	1.1	518	538	37
7	6.5	4.1	5.3	–	–	167	567	42
8	20.1	11.8	–	0.6	2.4	393	270	21
9	38.5	26.9	21.7	3.1	0.9	432	615	–
Average	26.3 ± 20.1	22.8 ± 14.3	14 ± 8.9	3.0 ± 1.8	15.0 ± 15.0	279 ± 143	613 ± 186	37 ± 10

cluded in 100% MCP home ranges ranged from 5.3–29 ha (mean 14 ha ± 8.9 ha, $n = 9$). The average size of MCP and Kernel home ranges was larger than the average clear cut size where weasels were tracked, which was 16 ha (range: 3–30 ha).

Mean overlap between daily home ranges for individual weasels ranged from 1.1% to 35.6%. There was bimodal variation in the degree of day-to-day site fidelity between weasels (Fig. 2, Table 3). Below we refer to weasels with high overlap between daily home ranges (mean $32.27 \pm 5.53\%$, $n = 3$) and short distances between daily centres of activity (147.83 ± 48.62 m, $n = 3$) as “residents” and to those with lower overlap between daily home ranges (mean $4.68 \pm 4.75\%$, $n=5$) and longer distances between daily centres of activity 379.7 ± 48.62 m, $n = 5$) as “transients” (Fig. 2).

Of the total 69 days of radio-tracking weasels spent 86% in a single clear cut without venturing into either adjacent forest or recently clear cut areas lacking grass cover. On 7 occasions (10% of days radio-tracked), however, weasels (no. 1, 4, 6, 7, 8, 9) were located after having left the original clear cut and having crossed a habitat lacking grass cover for at least 300 m. We tracked 4 weasels while 5 of these 7 movements were taking place (weasels no. 1, 4, 7, 9). On three additional occasions (4% of days radio-tracked), we tracked a weasel while it was

leaving a clear cut and entering low grass cover habitat (twice a mature spruce plantation, once either mature forest or a very recent clear cut without ground cover; weasels no. 1, 6, 9). Contact was lost from each of these 3 weasels as they left the clear cut too fast relative to our tracking ability. All these movements occurred during the daylight and are summarised in Table 4. Whenever weasels moved through habitats with little ground cover they used road verges, ditches, river banks or fire breaks, which provided some grass cover and step length was 4–5 times greater than when in a clear cut (Table 3, 4).

Factors influencing weasel movement

Weasel step length differed significantly between locations differing in grass composition (Kruskal-Wallis test: $\chi^2 = 14.99$, $df = 4$, $p < 0.01$; similar pattern found whether using starting or ending point of step) with weasels step length being greater the lesser grass cover the habitat provided (Fig. 3). There was a trend for weasels' MCP home range size to increase with the proportion of habitat 1 and 2, although a linear regression was non-significant ($B = 0.58$, $F_{1,6} = 3.46$, $p = 0.112$). There was no influence of vole density within a clear cut on total weasel Kernel home range size (linear regression: $F_{1,7} = 0.001$, $p = 0.98$), mean daily MCP home range size

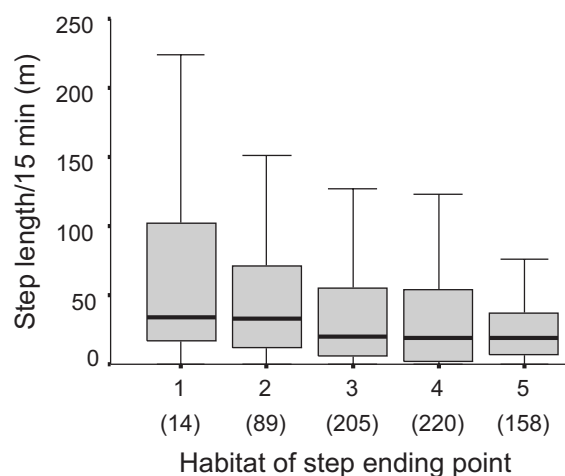


Fig. 3. Box-Plots for weasel step length per 15 min intervals plotted by habitat score of the ending point of steps. Steps are pooled for all weasels. Number in parentheses are sample sizes.

($F_{1,7} = 0.095$, $p = 0.77$) or MCP home range size after excluding the areas of habitat with less than 40 % grass cover ($F_{1,6} = 0.011$, $p = 0.17$). There was also no influence of field vole density within a clear cut on mean step length per 15 min ($F_{1,6} = 0.004$, $p = 0.95$), distance between centres of activity ($F_{1,7} = 0.196$, $p = 0.67$) or total distance travelled per day ($F_{1,7} = 1.083$, $p = 0.33$).

Discussion

In spite of their assumed central role in generating population cycles, little is known about the ranging behaviour, habitat preferences and movement characteristics of weasels in areas where voles experience population cycles. Even though our results only present a snapshot in time and relate to only males during the breeding season, so little is known, we are able to contribute valuable information.

Only if weasels were non-mobile relative to the scale of asynchrony in their vole prey population could weasel predation account for the prevailing spatial asynchrony in cyclic vole populations observed in KF. Based on the day-to-day site fidelity and the low recapture rate of

weasels in KF, we found a high proportion of probably transient male weasels within the population with one individual covering 800 m in little more than an hour. There is no evidence that handling of weasels might have caused unusual movement patterns, as weasels leaving a clear cut never did so the day of or after release but several days later. The observed pattern of movement seemingly reflects natural male weasel behaviour. It can thus be inferred that weasels located in a low vole density area would readily reach clear cuts with higher vole densities, which, based on the spatial pattern of vole dynamics, would be less than 7 km away. Weasels are thus unlikely to encounter food shortage in KF. This further supports Graham and Lambin's (2002) contention that weasels are unlikely to drive vole population dynamics in KF. While we stress that our results are restricted to males during the breeding season and that data on female movements would be desirable, there is no obvious reason why inherent mobility should constrain foraging by males or in females outside the breeding season, though females with dependent young are expected to show more space limited movements.

If prey availability determined spacing strategies of male weasels, it should also influence other movement parameters. Accordingly, weasels in a deciduous forest in Białowieża, Poland showed only very slight seasonal variation in home range size (16.1–24.1 ha and 6.5–25.6 ha during the breeding and non-breeding season respectively) but home ranges increased ten-folds when vole density crashed from up to 300 voles per ha in one year to only about 8 voles per ha in the following year (Jędrzejewski *et al.* 1995). Similarly, the tracks of least weasels and stoats (the latter being similar to British common weasels in size and probably diet) in western Finland were longest during the low phase and the decline phase of the vole cycle respectively (Klemola *et al.* 1999). However, differences between rodent densities in these studies were higher than the range of rodent densities in the present study (38–193 field voles per ha). This might explain why we did not find any influ-

ences of vole density on any of the weasels' movement parameters we studied. We also did not find any influence of prey density on weasel activity (Brandt and Lambin, 2005). However, prey density in KF might also have been above a putative threshold level below which it would constrain male weasel movement. This deduction is further supported by Erlinge's (1974) finding that common weasels were resident at field vole densities (30 field voles per ha) lower than our lowest estimates (38 field voles per ha). Even though it might be energetically more efficient in terms of foraging for male weasels to set up territories, the need to find receptive females might outweigh this necessity as long as prey density does not become critically low. McDonald and Harris (2002) observed pregnancies in female weasels on game estates in Great Britain between the 25th of April and 13th of October, which corresponds to the time we radio-tracked weasels. From comparison with other studies, we suggest that movement patterns of male weasels in this study reflected mate searching.

Although male weasel movement patterns were not detectably influenced by prey density, habitat choice was correlated with grass cover and hence field vole abundance but not with total rodent abundance. Diet analysis also confirms that weasels mainly feed on field voles as 83 % ($n=117$) of weasel scats with prey remains contained field vole remains (Lambin *et al.*, unpublished). Field vole numbers increased with the amount of grass cover the habitat provided, but no such relationship was found for wood mice and bank voles or total number of rodents. Weasels are known to also readily feed on bank voles and other rodent species (Erlinge 1975, Jędrzejewski *et al.* 1992, Pekkarinen and Heikkilä 1997, Sundell *et al.* 2003, and Elmeros 2006). However, prey choice of weasels might have been a consequence not a cause of weasel habitat choice made for other reasons. Weasels might have avoided habitats with lesser grass cover and presumably higher predation risk by avian predators and foxes that are known to prey on weasels (Korpimäki and Norrdahl 1989). Avoidance of predation risk is also a likely explanation for the longer step length in habitats with lesser grass cover, indicating that weasels trav-

elled through these habitats without hunting. Similar long step length in open habitats in farmland were reported by Macdonald *et al.* (2004) and Gehring and Swihart (2004). Indeed, we witnessed one of the weasels tracked being taken by a raptor when radio-tracked while it left a clear cut, and weasels account for approximately 1/300 prey found in fox scats in KF (Lambin *et al.*, unpublished). These results suggest that weasels in KF did not perceive their habitat as homogeneous but as patchy. Weasels focused their activities on areas with much grass cover and high field vole abundance showing that habitat structure influenced their movement.

The influence of habitat structure on weasel movement also becomes apparent when comparing weasel home ranges from different studies (Table 5). However, as our results represent minimum estimates due to the short time period over which weasels could be tracked, these comparisons must be treated carefully. The mean of 26.3 ± 20.1 ha for MCP home ranges of male weasels in KF was substantially smaller than the mean of 113.3 ± 57.9 ha for MCP home ranges of 4 adult males inhabiting farmland in southern England (Macdonald *et al.* 2004). Weasels seldom travelled far from linear features within their home ranges and thus utilised only a small proportion of the MCP areas (Macdonald *et al.* 2004). Although on a large scale, habitat in KF might be patchier than farmland habitat due to homogeneous large forest patches and varying aged clear cuts, within clear cuts the habitat was very homogeneous, as there was a great amount of grass cover such that weasels were not restricted to particular small-scale features such as fences or stone walls. As a result, size estimates for exploitable habitat have to be calculated in a different manner and our estimates for exploitable area within weasel MCP's (14 ± 8.9 ha) were larger than those found by Macdonald *et al.* (2004) (8 ± 1.1 ha). Male weasels radio-tracked in deciduous woodland in Poland had MCP home ranges between 11–37 ha during a rodent outbreak (Jędrzejewski *et al.* 1995), when rodent densities were similar but at times higher than during our study period in KF. Weasels were tracked in woodland with thick ground

Table 5. Overview of existing home range estimates and seasonal variation in movement patterns in *Mustela nivalis*. ? – no data.

Method	Prey species	Prey density (ind./ha)	Habitat	Home ranges (100% MCP) for males (ha)	Exploitable area within male home ranges	Home range (100% MCP) for females (ha)	Evidence for seasonal variation	Study
Telemetry	field voles	38–193	grassy clear cuts	26.3±20.1 (6.5–67.8, <i>n</i> =9)	14±18.9	?	only tracked in summer	this study
	yellow necked wood mice, bank voles	8–300	deciduous woodland	10.6–37.4 (<i>n</i> =5) during rodent outbreak, 117.4 and 215.8 ha (<i>n</i> =2) during rodent crash	?	?	only slightly larger home ranges in summer than in winter	Jędrzejewski <i>et al.</i> (1995)
	wood mice, bank voles	~2.6 wood mice, bank voles?	farmland	113±57.9 (58.5–192.6 ad, <i>n</i> =4) 18.3±5.4 (juv, <i>n</i> =3)	1.6±0.6 (juv) 8±1.1 (ad)	4.5–29.2 (<i>n</i> =3)	?	Macdonald <i>et al.</i> (2004)
	field voles	?	farmland	33.8±38.8 (11.9–38.5, <i>n</i> =7)	2.4	38 and 12 (<i>n</i> =2)	enlarged movement in spring/summer	Pounds (1981)
	?	?	vineyards, farmland, forest	resident: 7.49±10.24 (<i>n</i> =10) transients: 26.96±16.36 (<i>n</i> =6)	?	?	less residency in summer	Schmitt (2006)
Trapping	?	?	fragmented coniferous forest	wild weasels: 49.7±14.1 (<i>n</i> =4) released weasels: 14.6±5.4 (<i>n</i> =10)	?	released weasels: 27.1±25.8 (<i>n</i> =6)	?	Hellstedt and Kallio (2005)
	field voles	30–40	mixture of woodland, plantings and marshes		?	?	males roving in spring but territorial in late summer and autumn	Erlinge (1974)
	field voles	?		13.3±2.7 (88–142, <i>n</i> =7)	?	6.4 & 6.9 (<i>n</i> =2)	enlarged movement in spring/summer	Moors (1974)
	wood mice, bank voles	21–39	deciduous woodland	1.7–26.2 (<i>n</i> =7)	?	0.6–4 (<i>n</i> =3)	only one resident male weasel in summer, which increased home range compared to winter estimate	King (1975)
	voles	110–540	young plantation	1–5 (<i>n</i> =10)	?	?	slightly more overlap of home ranges during summer, but territoriaall year	Lockie (1966)

cover and were therefore probably also not restricted to limited areas within their home range, which might explain the similarity to our estimates. Thus we conclude that the structure of suitable habitat has important implications for weasel home range size such that more fragmentation leads to larger total home ranges with weasels covering much larger areas. Indeed, Oksanen *et al.* (1992) found a maximum distance of almost 10 km between the extreme points of daily weasel tracks in very patchy, low productivity tundra habitat. The patchy distribution of clear cut patches might contribute to a much higher predation risk, as weasels have to move through unsuitable habitat when searching for mates and might be required to increase their rate of movement, which in turn would increase their susceptibility to predation.

Although weasels were not seen using habitats with less than 40% grass cover, ten instances where weasels were found to enter the forest or a very recent clear cut without grass cover shows, that they clearly are capable of moving through those habitats. However, they moved much faster than through habitats with more grass cover. Weasels could easily reach adjacent clear cuts in KF in a single day (as mean nearest neighbour distance between nearest edges of clear cuts is only 177 m) (Sherratt *et al.* 2000) and are thus capable of rapidly tracking changes in field vole numbers. If weasels in KF were food limited and regulated vole population dynamics, their impact should therefore be synchronising on a rather large spatial scale at least during the summer. However, field vole populations are highly asynchronous in KF, adding support to the finding that cyclic dynamics in KF is not regulated by weasel predation. It therefore also seems unlikely that weasel populations in KF are regulated by their food supply. Our finding, including the observed aggressive interactions between weasels in KF resulting in weasels leaving the clear cut and our observation of a weasel being preyed upon by a raptor outside a clear cut lead us to hypothesise that predation and social factors could regulate weasel numbers in KF.

Conclusions

We showed that male common weasels in KF have relatively large home ranges compared to other studies and that there is possibly a high proportion of male weasels behaving nomadically during the breeding season. Weasels selected habitats with a high amount of grass cover and high field vole density. We could not resolve if this was an outcome of prey selection or predator avoidance and this remains to be further investigated. The scale of male weasel movement at the time of investigation was greater than the spatial synchrony of field vole densities in KF, which suggests that weasel predation is unlikely to cause the observed spatial patterns in field vole density.

Acknowledgements: We thank D. Tidhar for carrying out measurements on vole abundances and help with weasel catching and handling and S. Rao for tracking weasel no 9. We are also very thankful to W. Esser and M. Szwierczynski for much appreciated voluntary help with radio-tracking weasels and catching rodents and to G. Brown, L. Taylor and J. Fairbairn for help with weasel catching. K. Zub, F. Trillmich, C. M. King, two anonymous referees and J. Fairbairn provided comments that helped to improve the manuscript and we are very grateful to them. We thank the Forestry Commission for allowing access to study areas. This study was funded by the Natural Environment Research Council (NERC) and the German National Academic Foundation.

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Received 19 June 2006, accepted 14 November 2006.

Associate editor was Karol Zub.